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DETECTION OF TACTILE STIMULI. THRESHOLDS OF AFFERENT UNITS RELATED TO PSYCHOPHYSICAL THRESHOLDS IN THE HUMAN HAND

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SUMMARY

1. Psychophysical thresholds were determined at 162 points in the glabrous skin area of the human hand when slowly rising, triangular indentations of controlled amplitudes were delivered with a small probe. The method of constant stimuli was used with either the two alternative forced choice or the yes–no procedure. It was found that the distribution of the psychophysical thresholds varied with the skin region. Thresholds from the volar aspect of the fingers and the peripheral parts of the palm were low and their distribution was unimodal with a median of 11·2 μm. In contast, there was an over-representation of high thresholds when observations from the centre of the palm, the lateral aspects of the fingers and the regions of the creases were pooled, and the distribution was slightly bimodal with a median of 36·0 μm.

2. Nerve impulses were recorded from single fibres in the median nerve of human subjects with percutaneously inserted tungsten needle electrodes. The thresholds of 128 mechanosensitive afferent units in the glabrous skin area of the hand were determined when stimuli were delivered to partly the same points as stimulated for the assessment of the psychophysical thresholds. Of the four types of units present in this area the Pacinian corpuscle (PC) and rapidly adapting (RA) units had the lowest thresholds with medians of 9·2 and 13·8 μm, followed by the slowly adapting type I and slowly adapting type II units with medians of 56·5 and 331 μm. There was no indication of a difference between thresholds of units located in different skin areas.

3. In the region of low psychophysical thresholds there was good agreement between the thresholds of the rapidly adapting and Pacinian corpuscle units and the psychophysical thresholds, particularly at the lower ends of the samples. In the skin regions of high thresholds, on the other hand, practically all psychophysical thresholds were higher than the thresholds of the most sensitive afferent units. Moreover, simultaneous recording of nerve impulses during a detection task indicated that subjects did not detect stimuli strong enough to elicit several impulses in afferent units in this region.

4. Circumstantial evidence led to the conclusion that detection was dependent on one impulse in one or a few rapidly adapting units under optimal conditions in the region of low psychophysical thresholds, whereas it seemed unlikely that activity in Pacinian corpuscle units was crucial.

5. The findings are consistent with the interpretation that human subjects are able to detect an input consisting of a single impulse in a single rapidly adapting unit.

INTRODUCTION

Experiments on tactile sensibility in man and monkey suggest that the capacity of human observers to define a stimulus in psychophysical tests may bear a very close relation to the physiological properties of afferent units (Werner & Mountcastle, 1965; Mountcastle, Talbot & Kornhuber, 1966; Mountcastle, 1967; Talbot, Darian-Smith, Kornhuber & Mountcastle, 1968; Harrington & Merzenich, 1970). This interpretation suggests that processing within the central nervous system may be very simple and straight forward up to and including the level where perceptive experiences are produced. The development of a method for recording single unit impulses from human nerves has opened the possibility of studying relations between neural events in primary afferents and psychophysical responses in man. It seems likely that analyses of this type will allow more definite conclusions about the relationships between biophysical events and perceptive phenomena.

A cornerstone in sensory physiology and psychophysics is the concept of a sensory threshold. The absolute threshold may be defined as the minimal input signal giving rise to a response. It may be determined at different levels within a sensory system. The threshold of primary afferent units reflects the sensitivity at the lowest level whereas the psychophysical threshold reflects events at the higher levels of the system.

Neurophysiologists have produced support for the interpretation that the psychophysical threshold may be set by the properties of the peripheral sense organs (Hecht, Shlaer & Pirenne, 1942; Hensel & Bowman, 1960). Moreover, for the visual system it has been shown that the variability of the response which is always present in psychophysical detection studies might well be accounted for by a variability of the effective stimulus impossible to measure with sufficient exactness (Hecht *et al.* 1942). These conclusions are in marked contrast to views dominating the psychological literature, where it is usually held that a definite psychophysical threshold does not exist. Rather, it is claimed that any measurement of threshold gives a result largely dependent on central mechanisms and readily altered by contextual factors assumed to modify the subject's attitudes to the detection task and his decision task and his decision criteria (Swets, 1961; Green & Swets, 1966). It seems that these two views focus on a main issue in contemporary sensory physiology and psychophysics.

The present study is a test of the hypothesis that the thresholds of primary afferent units responding to tactile stimuli in the human hand match the psychophysical threshold to the same kind of stimuli.

Some aspects of the present findings have been published in preliminary reports (Vallbo & Johansson, 1976*a*, *b*).

METHODS

Two different sets of experimental data were collected; the psychophysical thresholds to tactile stimuli in the glabrous skin of the human hand and the thresholds of mechanoreceptive afferents innervating the same region. In some experiments the two thresholds were determined at exactly the same point, either simultaneously or successively. In other experiments, data on the two thresholds were collected from different points in the same subjects or from different subjects. One hundred and five experiments were conducted on seventy-six subjects (15–43 yr old; thirty-two females and forty-four males), seventy-one on psychophysical thresholds and sixty-eight on primary afferent fibres. The subjects were mostly medical students or members of medical professions and volunteered in the experiments which were performed according to the Declaration of Helsinki.

During an experiment the subject lay on a couch with the right arm extended from the body. The hand was embedded in a Plasticene (Colman) mould with the fingers moderately flexed. Fixation of the fingers was largely achieved by sticky clay or doublesided sticking tape attached to the dorsal surface of the finger. All kinds of distracting stimuli of the glabrous skin were avoided as much as possible. However, a metal band over the base of the little finger was fixed to the mould and served as an electrode for a floating circuit as will be described below.

Psychophysical threshold. The psychophysical threshold was determined with the method of constant stimuli and with either the two alternative forced choice or the yes–no procedure (Gescheider, 1976). In the two-choice procedure the beginning of the test period was indicated to the subject by an alarm light. Then two successive test intervals were specified by another two lights. The tactile stimulus was delivered randomly within one or the other of these two intervals and the subject's task was to press either of two buttons to indicate his preference with regard to which of the two intervals had carried the tactile stimulus. Chance performance in this procedure gives 50 % correct choices whereas any larger proportion indicates a sensory input guiding the subject's choice. In the yes–no procedure the beginning of the test interval was indicated to the subject by a clock and his task was to press a button if he thought a tactile stimulus had been delivered. The proportion of catch trials, i.e. test intervals which carried no stimulus, was mostly 0·5. Subjects were not informed about this proportion. In the yes–no procedure an equal proportion of correct yes-responses and false alarms indicates no detection whereas any higher proportion of correct yes–responses indicates a sensory input. However, in most experiments the false alarm rate was zero or very close to zero. Therefore psychometric functions were constructed by plotting the proportion of yes-responses against indentation amplitude and an ogive (the cumulative form of the normal distribution curve) was fitted to the data. The two-choice procedure was used in the majority of tests. However, when the psychophysical and the neural responses were studied in the same tests, the yes–no procedure was always used in order to allow a direct comparison between the two responses in the individual tests.

The stimulus amplitude was either varied semi-randomly from one test to the other or was held constant at a level close to the threshold of the afferent unit. The first strategy was mostly used with the two-choice procedure and the second with the yes–no procedure and when the neural threshold was similar or lower than the psychophysical threshold. When the threshold was determined at two different occasions or with the two different procedures the lowest value was always presented.

Subjects were not selected on the basis of their performance in detection tests and most had no experience of psychophysical tests prior to the experiment. At the beginning of an experiment a short period was spent on training to make the subject acquainted with the procedure and to make sure that he understood his task. A sound of moderate intensity was continuously present in the laboratory.

Neural threshold. Impulses were recorded from single afferent units in the median nerve with tungsten needle electrodes (Vallbo & Hagbarth, 1968; Vallbo, 1972) pecutaneously inserted about 10 cm above the elbow. Cutaneous mechanoreceptive units were classified into four types largely on the basis of their adaptation and receptive field properties (Knibestöl & Vallbo, 1970; Knibestöl, 1973, 1975; Johansson & Vallbo, 1979). The four types are rapidly adapting (RA), Pacinian corpuscle type (PC), and slowly adapting type I and type II respectively. The sampling of the units was largely random, possibly with the exception of a slight over-representation of units from the fingers. Units with a critical slope above 4 mm/sec were not included (see below).

The receptive field of an afferent unit encountered was scanned with test indentations to locate one or a few points of maximal sensitivity (Johansson, 1978). Then the threshold was determined at one of these points in either of two different ways. For 52 % of the units sufficient data were collected to allow the construction of a threshold curve (see below). For the other units the threshold was determined on line by defining the minimal amplitude of identation at which an impulse was elicited in approximately 50 % of eight to twenty tests. The amplitude of indentation was changed in steps of 0·4 μm for the most sensitive units whereas larger steps were used for the less sensitive units. Responses of a unit were independent of previous history when the stimuli were within the threshold range. Therefore it was not necessary to standardize the stimulus sequence with regard to ascending and descending stimulus intensities.

Forty-seven pairs of data on the two sets of thresholds were collected from exactly the same test points in the same subjects. When it was recognized that the threshold of an afferent unit was in the same range or lower than the psychophysical threshold the two sets of data were sampled simultaneously, i.e. the subject was asked to respond psychophysically to the stimulus and the associated responses of the single unit were recorded in each test. In other cases the psychophysical thresholds were determined either in the same experiment but when the single unit recording had been lost or on the next day. To ensure that exactly the same point on the skin was reached three small points of ink were tattooed in a triangle around the test point with needle pricks under visual control through a microscope and a sketch of the skin area was produced where the test point was indicated in relation to the tattoos, the skin ridges and the openings of the sweat glands.

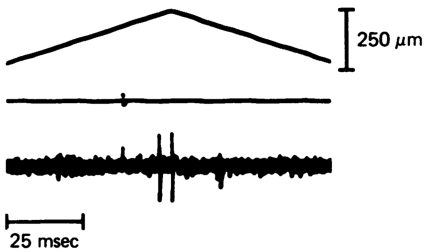

Fig. 1. Test stimulus for threshold measurements. Top trace shows probe movements, middle trace skin contact pulse (see text) and bottom trace signal recorded by electrode. In this test two impulses were elicited from a rapidly adapting unit by an indentation of 60 μm.

Mechanical stimulation. The test stimuli were triangular indentations delivered with a small probe having a shaft diameter of 0·45 mm and a hemispherical tip. The probe was actually an Amphenol micro-plug, type 221-759. The stimulation device has been described (Westling, Johansson & Vallbo, 1976). It consists of a moving coil system with feed-back control based on an optical transducer. A neon bulb supplied by a constant current served as the light source. The probe movement was set to start about 0·5 mm from the skin surface. When the probe made contact with the skin a floating circuit was closed and a triggering pulse produced. From this instant further movements of the probe proceeded for a preset time at a constant velocity of 4 mm/sec. Fig. 1 shows an example of a test stimulus illustrating the probe movement at the top, the skin contact pulse in the middle trace and the signal recorded by the intraneural electrode at the bottom. In this case two impulses from a rapidly adapting unit were elicited by an indentation of 60 μm. The described system for control of the true indentation amplitude was designed to take account of the inevitable movements of the skin surface with respiration and heart beats. Movements of this nature might amount to amplitudes 10 times the threshold amplitudes of the most sensitive mechanoreceptive units (cf. below) (Westling *et al.* 1976). The triggering pulse at skin contact (Fig. 1) was produced when the conductance in the floating circuit reached 11×10^{-11} mho. Precautions were taken to ensure that this conductance was reached at minimal physical contact between the probe and the skin. This was not always the case when the skin was very dry which was also manifested as a slow rise of the conductance. To control this source of variability the time derivative of the conductance change was checked in each test and if the maximal derivative was too low the test was rejected. In some experiments the skin was moistened initially with a solution of 10% glycerin in water to decrease the resistance. The solution was allowed to penetrate into the skin so that no fluid was present on the surface when the tests were performed. With these precautions it was estimated that the error of indentation due to variation in triggering was less than 0·001 μm.

The stimulating device was mounted on a heavy semicircular bronze frame and could be moved along it with a cog-wheel. The frame could be tilted and also moved in the horizontal plane so that most areas of glabrous skin could be reached with the probe perpendicular to the skin surface.

The target point on the skin surface was carefully controlled with the aid of a dissecting microscope at 25 or 40 times magnification and any movements of the subject's hand were compensated for. It was still difficult to guarantee that the probe hit exactly the same point in all tests of a series as the hand moved almost continuously by some tens of microns. It was felt that this factor accounted for some of the variability of the responses, not only in the afferent units but of the subjects' psychophysical responses as well.

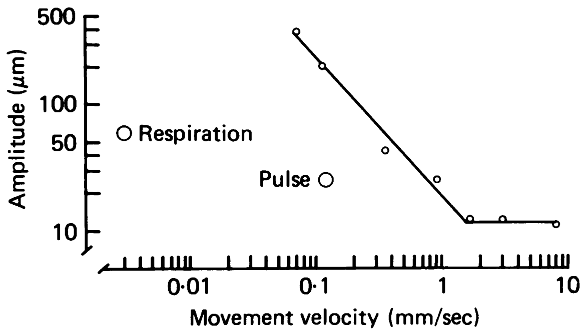

Fig. 2. Psychophysical threshold as a function of velocity of probe movement. Small circles indicate experimental threshold data. Line drawn by eye. Large circles, approximate amplitudes and velocities of perpendicular movements of the skin surface due to respiration and pulse beats.

The method of mechanical stimulation used in the present study was designed on the basis of information in the literature as well as preliminary experiments which showed that the psychophysical threshold was dependent on several contextual factors. Control experiments indicated that a pre-indentation of 0·25–0·5 mm might decrease the threshold by a factor of 3–5. Moreover it was found that sustained deformation of the skin in the vicinity of the test point, e.g. with a metal clamp over the finger, might increase the threshold by a factor of 6. The slope of indentation has been shown to have pronounced effects on the psychophysical threshold (Darlington & Donaldson, 1973; Lindblom, 1974).

Fig. 2 shows that the threshold is largely independent of the slope in the range above 2 mm/sec, whereas it increased rapidly at lower velocities. The velocity used in the present study was 4 mm/sec so the minor variation around this velocity occurring in the whole series of experiments (range 3·92–4·44 mm/sec) was not a source of error as long as the absolute indentation amplitude was measured correctly. In Fig. 2 are also indicated for comparison, the approximate amplitudes and maximal velocities of movements of the skin surface due to respiration and heart beats. These movements vary between subjects and between test points in the same subject. Attention should therefore be paid to the order of magnitude rather than the exact figures. However, the findings clearly indicate that a method of controlling the *effective* indentation amplitude and not only the probe movement is required when tactile thresholds are studied. However, it is obvious from Fig. 2 that the velocities of skin movements with respiration and heart beats are low in relation to the velocity of the stimulus ramp. It was estimated that the variability of effective skin indentation due to pulsations did not exceed about 2·5 % whereas the effect of respiratory movements was even less. Yet the pulsations were the main source of error of stimulus amplitude (Westling *et al.* 1976).

Mathematical and statistical methods. The cumulative form of normal probability curves were fitted to the threshold data by a method of maximum likelihood estimation (Uvell, 1975). A procedure of this nature was required when the threshold of an afferent unit was determined, because the number of the tests could not be standardized but was dependent on the duration of successful recording from the single unit. In the present study the midpoint of the probability curves fitted to the experimental data will be considered whereas other aspects will not be presented. It should be pointed out that the statistical error in the assessment of the midpoint of the curves was within ± 10 % of the threshold value in most cases.

Non-parametric statistics were used to describe the characteristics of the unit populations (e.g. Siegel, 1956). The statistical significance of differences between two populations was assessed using the Mann-Whitney U test. When more than two populations were considered the Kruskal–Wallis one way analysis of variance was used. The association between two variables was assessed by means of testing the significance of the Spearmans rank correlation coefficient. The level of probability selected as significant was a value of $P < 0{\cdot}1$.

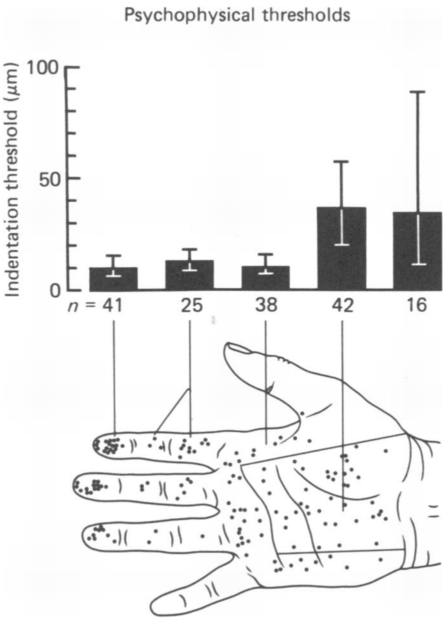

Fig. 3. Psychophysical thresholds in various regions of the glabrous skin area. Test points are indicated in drawings of the hand. From left to right the columns show data from the terminal phalanx, the middle and basal phalanges, the peripheral part of the palm as indicated in the drawing and detailed in the text, the central part of the palm, and, to the extreme right, data from the lateral aspects of the fingers and the regions of the creases taken together. Column heights give medians and bars 25th and 75th percentiles.

RESULTS

Psychophysical thresholds. The psychophysical thresholds were determined at 162 points in fifty-one subjects. Most test points are shown in Fig. 3. There was a relative over-representation of high thresholds in certain skin regions whereas the values were more uniform in others. High thresholds were common on the lateral aspects of the finger, in the creases and in the centre of the palm. The columns in Fig. 3 give the median values as well as the interquartile distances for the samples from the various regions as indicated in the drawing and detailed in the legend. A central area of the palm was delimited by the distal crease and two imaginary lines. One line was drawn as an extension of the fourth inter-digital space from the distal crease and parallel to the long axis of the hand. The other line was drawn from the point of intersection between the second inter-digital space and the distal crease in the palm to the point of the angle between the forearm and the first metacarpus. Sixteen test points located in the creases and on the lateral aspects of the fingers are not indicated in the drawing of the hand.

The median values as well as the interquartile distances were considerably higher for the samples collected from the centre of the palm, the lateral aspects of the fingers, and the creases than in the other regions. The differences between the various other regions of the hand were very small. No significant difference was found in statistical analysis between any of the other regions.

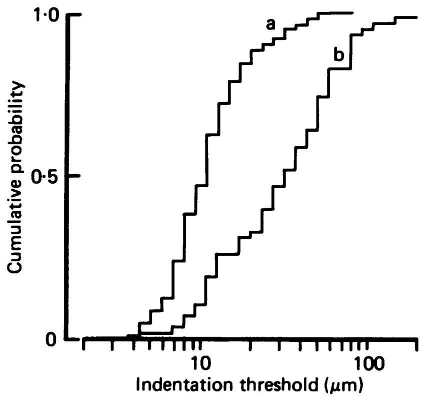

Fig. 4. Psychophysical thresholds in two different regions of the glabrous skin area. Left-hand curve presents data from the volar aspects of the fingers, between the regions of the creases, and the peripheral part of the palm. Same data as shown in the three left-hand columns of Fig. 3. The right-hand curve presents data from the central part of the palm, the lateral aspects of the fingers and the regions of the creases. Same data as in the two right-hand columns of Fig. 3.

On the basis of these findings it seems justified to consider two separate regions in the human hand: (1) the volar aspects of the fingers and the peripheral parts of the palm with the exception of the creases, where the psychophysical thresholds were fairly uniform and low; and (2) the centre of the palm and the lateral aspects of the fingers, where many thresholds were considerably higher, as they also were in the creases. To simplify the discussion these two regions will be denoted the low threshold region and the high threshold region, although it should be borne in mind that a fair proportion of low thresholds were found in the high threshold region and vice versa.

The total sample of psychophysical thresholds (162 points) is presented in Fig. 4 where data from the high and low threshold regions are shown separately. The curves illustrate that the two samples differ drastically. The medians were 11·2 and 36·0 μm and the distances between the 25th and 75th percentiles 7·4 and 44·1 μm. From frequency distributions of the samples (not illustrated) it was obvious that the sample from the low threshold region was unimodal with a peak at about 10 μm and approached a log normal distribution. In contrast, there was a tendency to bimodality in the sample from the high threshold region with one peak close to 10 μm and another one at about 50 μm. The bimodality of the sample from the high threshold region was partly related to the location of the test points within this region. Low thresholds were more common at points located towards the periphery of the central palm area and on the opposing surfaces of the thumb and index. For instance the three lowest thresholds found on the lateral aspects of the fingers were on the ulnar aspects of the thumb and the radial aspect of the index. These skin areas might have a higher significance as sensory regions in man than the other lateral aspects of the fingers.

The threshold values produced by individual subjects were analysed to elucidate whether inter-subject differences accounted for the variability seen in Figs. 3 and 4. The threshold values from twelve subjects who were tested at more than three points are shown in Fig. 5. The histograms are arranged in order from samples with low

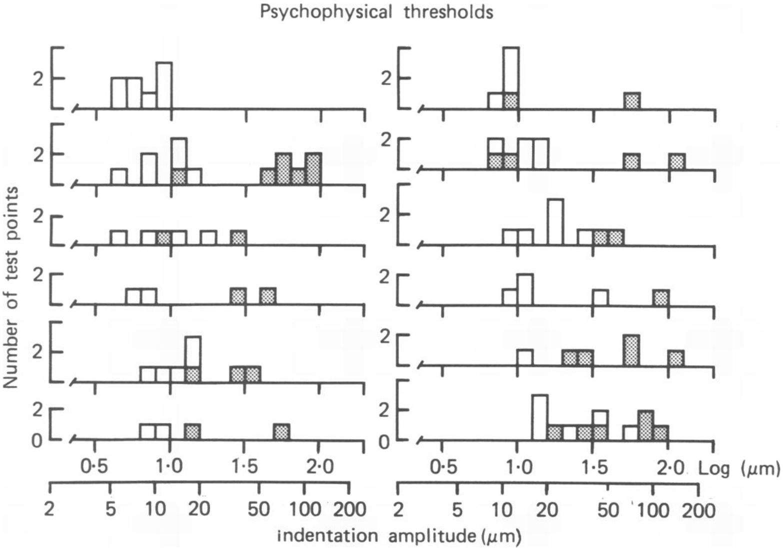

Fig. 5. Psychophysical thresholds assessed in twelve subjects tested at more than three points. White and shaded areas refer to the two skin regions with low and high psycophysical thresholds, as detailed in text.

medians to samples with high medians. Open and filled blocks represent data from the low and the high threshold region. Considering values from the low threshold region it is obvious that there is a clear inter-subject variation in these samples as some subjects produced mainly thresholds below 10 μm whereas others produced mainly higher thresholds. It is not possible to assess whether these differences are simply an effect of location of test points because the samples are too small. They might also reflect true differences in neural mechanisms between subjects or varying performance because of inadequate attention to the task. The latter alternative seems likely to be a contributing factor also to the variability in the total sample as the subjects were totally unselected. Generally, it seems therefore reasonable to pay more attention to the lower threshold in the total sample than to the higher ones.

Another question is whether the dominance of high values found in the high threshold regions in the main sample is due to these values being collected from subjects who generally produce high thresholds. This seems unlikely as a difference of the same kind as in the total sample was present for practically all the individuals represented in Fig. 5.

Threshold of mechanosensitive afferent units. The indentation thresholds of 128 units are presented in Fig. 6. The curves give the relative frequency of occurrence in the cumulative form of the four separate unit types. The sample of each unit type was split into two groups on the basis of the location of the receptive fields. The continuous and interrupted lines represent units with fields in the regions of low and high psychophysical thresholds respectively. It may be seen that there were no major differences between afferents' thresholds from the two regions, as the two sets of curves are very close. Statistically, no significant differences were found for any of the unit types.

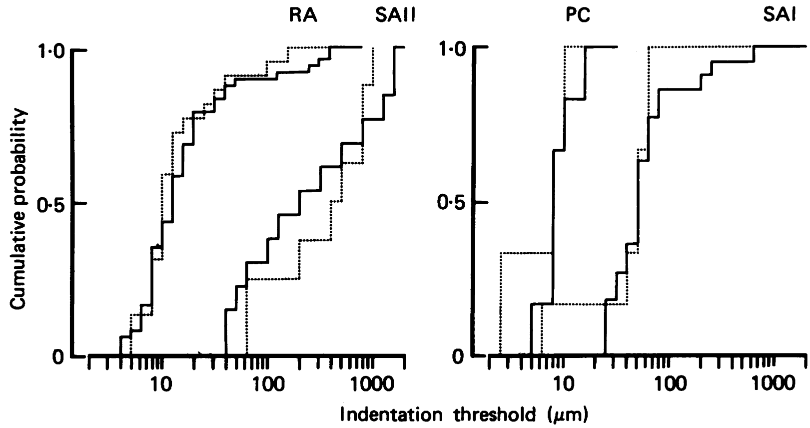

Fig. 6. Thresholds of the four types of mechanosensitive afferent units in the glabrous skin area. Continuous and interrupted lines refer to data from the two skin regions with low and high psychophysical thresholds respectively. RA, rapidly adapting; SA, slowly adapting types I or II; PC, Pacinian corpuscle.

Similarly in a larger sample tested for their thresholds with von Frey's hairs (284 units) there were no differences between the distribution of thresholds of the afferent units sampled from the high and low threshold regions (Johansson, R. S. & Vallbo, Å. B., unpublished).

Fig. 7 demonstrates the similarity between the thresholds of the afferent units from different skin regions. The columns and the bars at the top show the medians and the interquartile distances separately for the rapidly (RA and PC) and the slowly adapting unit groups. It may be seen that there were no pronounced differences between the six regions except in one single case. Statistical analysis indicated that the differences were not significant except for the slowly adapting units in the peripheral part of the palm.

It is also obvious from Fig. 6 that the rapidly adapting (RA) and Pacinian corpuscle (PC) units had the lowest thresholds of the four types with median values of 13·8 and 9·2 μm. The difference between the samples of these units was statistically significant. The thresholds of the most sensitive rapidly adapting and Pacinian corpuscle units were 4·0 and 2·6 μm respectively. The slowly adapting type I units had considerably higher thresholds except for a single unit at 6·9 μm. In the slowly adapting type I sample the median value was 56·5 μm, whereas the slowly adapting type II units had the highest thresholds of the four types with a median value of 331 μm.

The same ranking with regard to thresholds between the four unit types was found in the larger sample (284 units) tested for their thresholds with von Frey's hairs (Johansson, R. S. & Vallbo, Å. B., unpublished).

The distributions were mostly assymmetrical with an over-representation of high values although this is not all that obvious from Fig. 6 because of the logarithmic abscissae. An exception was the Pacinian corpuscle sample which seemed more symmetrical.

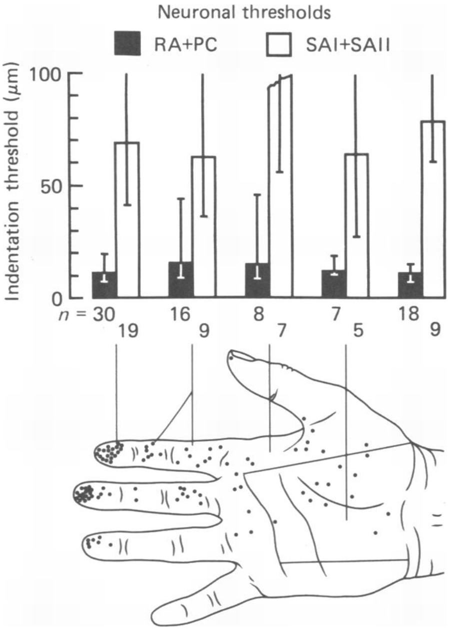

Fig. 7. Thresholds of afferent mechanoreceptive units in various regions of the glabrous skin area. This Figure has a similar design as Fig. 3 where details are given in the legend. The dark and white columns refer to the two types of rapidly adapting units and the two types of slowly adapting units respectively.

It should be emphasized that the samples of Fig. 6 do not include units with critical slopes above 4 mm/sec which were excluded because they would not contribute to the afferent signal in the psychophysical tests. In an unbiassed sample as many as 61·9 % of the Pacinian corpuscle units and only 5·2 % of the rapidly adapting units had higher critical slopes.

The relation between neural and psychophysical thresholds. A comparison between the data presented in Figs. 3 and 4, on the one hand, and those in Figs. 6 and 7, on the other, allows some conclusions with regard to the role of the different types of afferent units for psychophysical detection. Particular attention will be paid to the lower range of psychophysical thresholds. In the low threshold region about 40 % of thresholds fall below 10 μm. Only the two types of rapidly adapting units are sensitive enough to provide an afferent signal in response to these small stimuli. The slowly adapting units had considerably higher thresholds except for a single type I unit located in the palm.

To facilitate a direct comparison between psychophysical thresholds and the thresholds of the rapidly adapting and Pacinian corpuscle units Fig. 8 was constructed. It shows the psychophysical thresholds from the low threshold region and the total sample of both unit types collected from the whole glabrous skin area. There is good agreement between the three curves at the lower end. The fact that the curve for the Pacinian corpuscle units extends to lower values than the other two curves might not deserve emphasis as it is accounted for by a single observation. Thus it may be concluded that the detection of these stimuli was due to either the rapidly adapting, the Pacinian corpuscle units, or both.

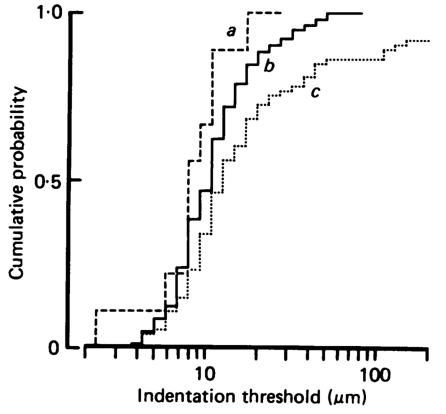

Fig. 8. Thresholds of mechanosensitive afferent units compared with psychophysical thresholds. Curve *b* shows the psychophysical thresholds. Curves *a* and *c* show the thresholds of the total sample of Pacinian corpuscle units and rapidly adapting units respectively.

The finding that neural thresholds did not extend to lower values than the psychophysical thresholds is of considerable theoretical significance with regard to the concept of a psychophysical threshold (Green & Swets, 1966) as will be discussed below.

In the region of high psychophysical thresholds the afferent units were as sensitive as in the region of low psychophysical thresholds (Fig. 6). In contrast the psychophysical thresholds were considerably higher in the former region (Figs. 3 and 4). Only a small fraction of psychophysical thresholds were below 10 μm and the majority of these were found on opposing aspects of the thumb and the index finger and in the periphery of the central region of the palm. Thus it seems unlikely that stimuli giving rise to a minimal excitation of the most sensitive afferent units were detected psychophysically in the high threshold region.

Comparison between neural and psychophysical thresholds measured at the same target points. The line of reasoning pursued in the previous section suggests that a minimal input from the most sensitive afferent units may be detected by human subjects when the stimuli are delivered to the volar aspects of fingers and in the periphery of the palm On the other hand, it seems that such minimal inputs are not detected when originating from the centre of the palm or the lateral aspect of the fingers. It may be argued, however, that failure of the subjects to detect stimuli in the region of high psychophysical thresholds is due to the low density of afferent units in this region (Johansson & Vallbo, 1979). If the highly sensitive units in this region are very few, the probability of hitting one of them is low. It will be shown below, however, that the high thresholds were not due to a dearth of units responding to the test stimuli.

Fig. 9 shows thirty-four pairs of data collected when the psychophysical and neural thresholds were determined at the same test points. Such pairs were collected when it was preliminarily observed that an afferent unit had a similar or lower threshold than the psychophysical threshold. Fig. 9 *A* and *B* show findings from the regions of low and high psychophysical thresholds respectively. The thick line indicates equality

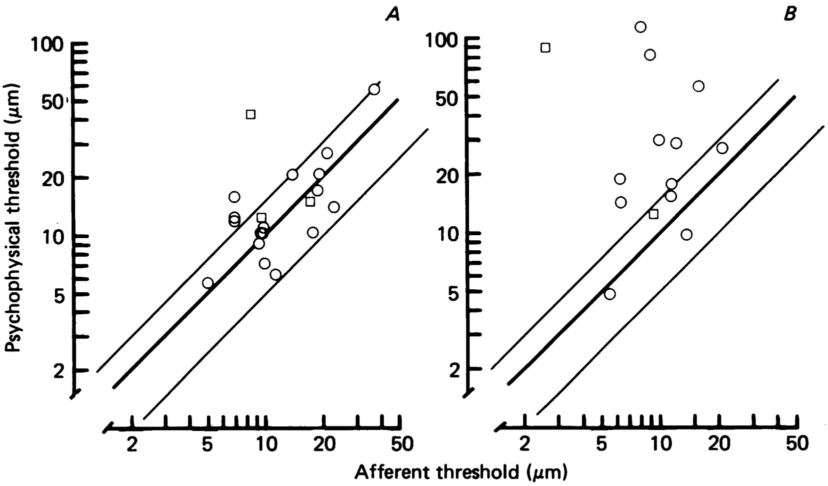

Fig. 9. Comparison between psychophysical thresholds and thresholds of mechanosensitive afferent units when tested at identical target points. *A* and *B* refer to data from the two skin regions with low and high psychophysical thresholds. Thick lines indicate equality and thin lines delimit the region where points fall when the psychophysical threshold is within ± 50 % of the threshold of the afferent unit. Circles and squares represent data from rapidly adapting and Pacinian corpuscle units.

and the two thin lines delimit the region of the plot where points would fall when the psychophysical threshold is within ± 50 % of the neural threshold. Only points which fall above the − 50 % line were included in the plot. It seemed that data concerning points located far below the line of equality would illustrate a trivial finding, namely that other units with lower thresholds were excited in addition to the one whose impulses were recorded. Consider (1) pairs with a psychophysical threshold within ± 50 % of the neural threshold, and (2) pairs with higher psychophysical thresholds. In the low threshold region (Fig. 9*A*) the proportions of the two types were 80/20. The one point with a psychophysical threshold 5 times higher than the neural threshold originated from a Pacinian corpuscle unit. In the high threshold region the corresponding proportions were 36/64 (Fig. 9*B*). For one target point with a Pacinian corpuscle unit the psychophysical threshold was about 25 times higher but also for several points with rapidly adapting units the discrepancies were considerable.

It was often noticed during the experiments that many stimuli in the region of high psychophysical thresholds and not detected by the subject elicited several impulses in the single unit recorded. It is obvious that a considerable number of impulses must have been evoked by the stronger stimuli because it has been shown that two and three impulses are produced in the most sensitive afferents at indentation amplitudes of 20 and 40 μm respectively (Vallbo & Johansson, 1976*a*).

These findings clearly indicate that there exist within the region of high psychophysical thresholds units excited when stimuli not detected psychophysically were delivered. It seems unlikely therefore that the higher thresholds in this region are due to absence of units responding to the indentations.

Estimates of number of units excited at the psychophysical threshold. The findings reported above clearly demonstrate that one impulse in the most sensitive rapidly adapting and Pacinian corpuscle units constitute a signal which may be detected

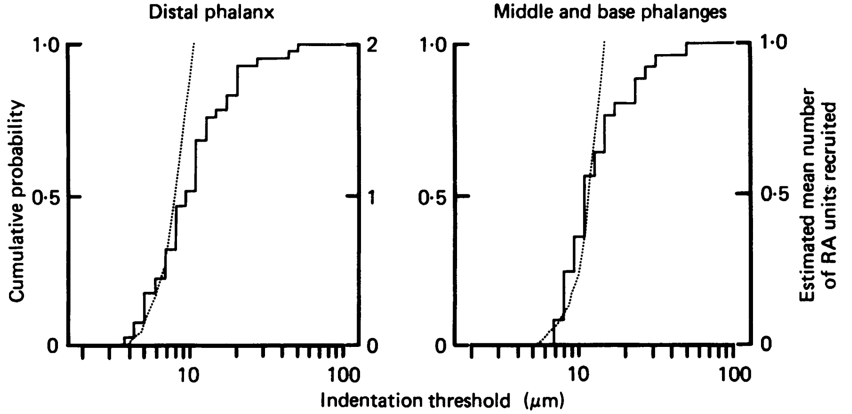

Fig. 10. Comparison between psychophysical thresholds and estimated number of rapidly adapting (RA) units activated as a function of indentation amplitude on the terminal phalanx (left-hand diagram) and on the middle and the basal phalanges (right-hand diagram). Continuity lines give the psychophysical thresholds (left-hand ordinates) and interrupted lines the estimated average number of rapidly adapting units activated (right-hand ordinates). Note the difference between the two right-hand ordinates.

psychophysically. It is not possible, however, to assess experimentally how many units are excited at the minimal psychophysical thresholds. Fig. 10 was constructed to elucidate this particular question. The continuous lines show psychophysical thresholds in the low threshold region and the dotted curves show estimates of the average number of rapidly adapting units excited as a function of the amplitude of skin indentation for two different skin regions, the finger tip (Fig. 10 left) and the middle and basal phalanges (Fig. 10 right). The estimates are based on experimental data on the distribution of thresholds, density of units and sizes of their receptive fields. The procedure has been described in detail (Johansson, 1979). The diagrams show that the average number of rapidly adapting units activated on the finger tip does not exceed 0·5 in the range of stimulus intensities where about 25 % of the psychophysical threshold values fall. The corresponding figure for the middle and basal phalanges was about 50 %. Unfortunately an adequate estimate for the two regions in the palm could not be done on account of the small sample of units. The same was true for the Pacinian corpuscle unit samples. But it may be intuitively appreciated that the corresponding figure for the Pacinian corpuscle units would be in the same range as for the rapidly adapting units or smaller since the effect of the low density of Pacinian corpuscle units would only partly be cancelled by their lower thresholds and the larger size of their receptive fields (Johansson & Vallbo, 1979). Thus the estimates indicate that the number of units excited by stimuli at the minimal psychophysical thresholds is small and probably just one in many cases. A similar conclusion has been advanced by Hensel & Bowman (1960) for hair follicle receptors on the dorsum of the hand, although their conclusion seems to be based on qualitative observations on the sensitivity of only one afferent unit.

DISCUSSION

The hypothesis tested in the present study was whether the ability of human subjects to detect minimal tactile stimuli is limited by the sensitivity of the peripheral sensory apparatus or whether the psychophysical capability is set by central mechanisms. The hypothesis was tested by comparing the neural and the psychophysical thresholds. Any similarity or discrepancy between the two kinds of thresholds are not due to the stimulation technique because the same method of stimulation was used in the assessment of the two kinds of thresholds.

The strategy of the present detection analysis is almost the opposite of that in many other psychophysical detection studies where a noise is deliberately mixed with the test stimuli (Green & Swets, 1966). Experimental analysis of absolute threshold, by definition, requires a strategy similar to the one used in the present study where the noise in the device producing the test stimuli was reduced as much as possible.

Studies of the absolute psychophysical threshold in the glabrous skin of primates have provided varying results when expressed in units of amplitude of indentation (Franzén & Offenloch, 1968; Darlington & Donaldson, 1973; Rollman, 1973, 1974; Lindblom, 1974; Lindblom & Lindström, 1976; Vallbo & Johansson, 1976*a*). The same is true for the threshold of the afferent units (Lindblom, 1965; Lindblom & Lund, 1966; Knibestöl, 1973, 1975).

There are a number of indications in the literature that the great variance of thresholds found in psychophysical as well as neurophysiological studies may to a large extent be accounted for by varying stimulus parameters. It seems doubtful therefore, whether it is reasonable to analyse the relation between the two kinds of threshold values unless they have been extracted with exactly the same method of stimulation.

Studies on vibrotactile thresholds indicate that there are two different mechanosensitive systems as first emphasized by Verrillo (Verrillo, 1963, 1968; Talbot *et al.* 1968; Mountcastle, Talbot, Sakata & Hyvärinen, 1969; Mountcastle, LaMotte & Carli, 1972). One system is particularly sensitive in a higher frequency range. Other characteristics are that it is a summating system in the sense that the threshold decreases when the area stimulated increases and it is very sensitive to preindentation. It seems likely that this system is dependent on Pacinian corpusle (PC) units. The other system is more sensitive in a lower frequency range, is non-summating and not as much dependent on preindentation. It seems likely that this system is dependent on rapidly adapting (RA) units. Much of the variation in absolute psychophysical thresholds reported in the literature is possibly due to different stimulation techniques preferentially exciting afferent units belonging to one system or the other.

The stimulation technique used in the present study was designed to excite a minimal number of afferents and to guarantee as far as possible a 'clean' background for the test stimuli. The technique favours any system that is non-summating and independent of pre-indentation which was also the intention behind the design. This strategy forced the development of a stimulus device considerably more complicated than many others (Westling *et al.* 1976). It has been shown, however, that the method is adequate for stimulation of single end organs (Johansson, 1978).

Within certain skin regions of the hand there was a close similarity between the thresholds of the most sensitive rapidly adapting and Pacinian corpuscle units and the lowest psychophysical thresholds, justifying the conclusion that either or both of these two unit types account for the detection of minimal stimuli whereas the slowly adapting units do not. It was not possible to produce conclusive evidence for a choice between the rapidly adapting or the Pacinian corpuscle units. However, there are some indications that the rapidly adapting units are the crucial type of afferent units. A very striking observation supporting this conclusion, but one which is difficult to document, is that the exact target point was often very critical for the psychophysical threshold. It has been shown that this is true also for the threshold of the rapidly adapting units but not for the Pacinian corpuscle units (Johansson, 1978). Another indication is that a very good agreement between the presence of an impulse in a single unit and a positive psychophysical response in single tests was found for some rapidly adapting units (Vallbo & Johansson, 1976*a*) but never for a Pacinian corpuscle unit. On the contrary, occasionally one of the latter was found which responded with several impulses while no detection was reported by the subject although he was forcefully asked to pay maximal attention to the task. It may be added that the same subject when tested at other target points produced equally low psychophysical thresholds as the majority of subjects. A third indication that the rapidly adapting units are the essential ones for the detection of the tactile stimuli used in the present study is that vibrotactile studies suggest that detection through the Pacinian corpuscle system requires summation (Verrillo, 1968), whereas the present stimuli probably give very little summation and were designed to excite a minimal number of afferent units.

It was demonstrated that there are two regions of the glabrous skin with different psychophysical characteristics. (1) On the volar aspects of the fingers and the peripheral and elevated parts of the palm, psychophysical thresholds were generally low and of the same magnitude as the thresholds of the rapidly adapting and Pacinian corpuscle units. It seems that these areas are particularly significant for tactile sensibility because contact with external objects is primarily made with these areas in manipulation and exploration. (2) In the centre of the palm and on the lateral aspects of the fingers and in the creases, psychophysical thresholds were mostly considerably higher than the thresholds of the rapidly adapting and Pacinian corpuscle units in the area. Thus it seems that an afferent signal is analysed more accurately in the central nervous system when it originates from the tactually most significant skin regions.

The findings of the present study complement the results presented in a previous one on the peripheral organization of the tactile mechanisms (Johansson & Vallbo, 1979) and the two demonstrate that there is a differentiation in peripheral as well as in central parts of the somatosensory system subserving tactile sensibility in the human hand.

Two findings are of particular interest with regard to the theory of a psychophysical threshold. The signal detection theory postulates, within the sensory system, a noise which is large in relation to the minimal afferent input. In contrast, one conclusion arrived at in the present study was that a single impulse in a single afferent unit, may stand out of any noise there may be in the central part of the somatosensory system. Moreover, it was found that the sample of afferent thresholds did not extend to lower values than the thresholds obtained with the two alternative forced choice procedure and the yes–no procedure when a minimal proportion of false alarms was produced. This finding also indicates that a minimal afferent input gives rise to a sensory signal which does not merge with a noise distribution within the central nervous system, but subjects are capable of separating the two under optimal conditions.

These two conclusions indicate that the noise level is small in relation to the minimal sensory signal in certain parts of the system as opposed to a central postulate of the signal detection theory. However, it should be emphasized that these conclusions do not generally invalidate the signal detection theory as employed in psychophysical threshold studies. They rather support 'the concept of a high threshold located near the upper end of the noise distribution' (Gescheider, Wright, Weber & Barton, 1971; Eijkman & Vendrik 1963; Vendrik & Eijkman, 1968) in some parts of the somatosensory system. It might also be of interest to point out that 'the rise of the signal detection theory...has...led to an almost complete lack of attention to the analysis of basic noise-free detection phenomena' (Corso & Norman, 1973) whereas the present study was focussed on these particular kinds of phenomena.

With regard to the hypothesis tested in the present study the findings indicate that the limit of detection is set by the sensitivity of the peripheral organization for the tactually most significant skin regions and by central mechanisms for tactually less significant regions. Perhaps maximal precision in central analysis requires too elaborate a system to be worthwhile except for the skin regions of maximal tactual significance.

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